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Ulrich R. Bernier
University of Florida, ubernier@gainesville.usda.ufl.edu

Kay D. Furman
USDA-ARS

Daniel L. Kline
USDA-ARS

Sandra A. Allan
USDA-ARS

Donald R. Barnard
USDA-ARS

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ULRICH R. BERNIER, KAY D. FURMAN, DANIEL L. KLINE, SANDRA A. ALLAN, AND DONALD R. BARNARD

USDA–ARS, Center for Medical, Agricultural, and Veterinary Entomology, 1600 SW 23rd Drive, Gainesville, FL 32608

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ABSTRACT Nepetalactone, the primary component of catnip oil, was compared with the repellent *N,N*-diethyl-3-methylbenzamide (deet) for its ability to affect the host-seeking ability of *Aedes aegypti* (L.). A triple cage olfactometer was used to bioassay each substance and to assess its attraction inhibition (spatial repellent) attributes when combined with the following attractants: carbon dioxide, acetone, a blend of L-lactic acid and acetone, and human odors. Repellent tests were conducted with each substance against female *Ae. aegypti*, *Anopheles albimanus* Weidemann, and *Anopheles quadrimaculatus* Say. Catnip oil and deet were both weakly attractive to *Ae. aegypti*, catnip oil was the better spatial repellent, whereas deet was a more effective contact repellent in tests with all three species of mosquitoes.

KEY WORDS olfactometer, inhibition, nepetalactone, repellents

CATNIP, *Nepeta cataria* L., is a member of the mint family (Lamiaceae) that is used as a food additive, in traditional medicine, and as a stimulant for felids (Tucker and Tucker 1988, Leung and Foster 1996). One possible basis for the use of catnip by felids might be for defense against mosquito attack (Weldon 2003, Weldon et al. 2003), and if so, other species, e.g., humans, may benefit from this means of protection against predators by concealment or cloaking of odors (Eisner et al. 1978). Nepetalactone, a primary component of catnip oil, has been reported recently to repel cockroaches (Peterson et al. 2002) and mosquitoes (Peterson 2001).

Synthetic and natural products have been evaluated as repellents throughout the years (Peterson and Coats 2001), and *N,N*-diethyl-3-methylbenzamide (deet) is one of the most successful (McCabe et al. 1954). In laboratory-based sensory physiology studies, deet inhibits favorable response to mosquito attractant(s), such as L-lactic acid as a host attractant for *Aedes aegypti* (L.) (Davis and Bowen 1994) and ethyl propionate as an oviposition attractant (Kuthiala et al. 1992). Two neuron classes of the antennal grooved pegs on *Ae. aegypti* are reported to respond to lactic acid, possible skin acids, and essential oils, and these also are inhibited by deet (Davis and Bowen 1994, Sutcliffe 1994). Deet not only affects cells responsible for detection of attractants but also inhibits cells that are not involved in the detection of attractive host odors (Boeckh et al. 1996).

Less attention has been directed toward the discovery of spatial repellents (synonymous here with attraction inhibitors; Kline et al. 2003) compared with the discovery of topical repellents (Gouck et al. 1967, Schreck et al. 1970). Hoffmann and Miller (2002, 2003) demonstrated spatial repellency attributable to vapor phase release of deet. Attraction inhibitors have a primary effect that results in a reduction of the number of mosquitoes that take flight in the presence of an attractant; this is accomplished possibly by masking the attraction at a cellular level. Because a totally effective inhibitor has yet to be discovered, a percentage of mosquitoes are still activated to flight upon detection of attractive odors even in the presence of an inhibitor. However, these mosquitoes have greater difficulty orienting to and locating the attractive odor source compared with mosquitoes in the absence of an inhibitor (Kline et al. 2003).

A Feinsod & Speilman olfactometer (Feinsod and Spielman 1979) modified to identify attractants, inhibitors, and repellents was used to demonstrate inhibition of mosquito host-seeking behavior by deet (Dogan and Rossignol 1999, Dogan et al. 1999). In our triple cage, dual-port olfactometer system (Posey et al. 1998), we test for attractants and can test for attraction inhibition by combination of the candidate inhibitor with established attractants (Bernier et al. 2001). Peterson (2001) found that in laboratory bioassays with a glass tube olfactometer, *Ae. aegypti* were less likely to land on the side that contained deposited nepetalactone compared with the side that had deet.

This paper reports the results of research only. Mention of a chemical compound does not constitute an endorsement for use by the USDA, nor does it imply registration under FIFRA as amended.

The same work also demonstrated that a higher dosage of deet was required to be as effective as a lower dosage of nepetalactone. Stimulated by this work, we compared commercially available catnip oil with deet by using our protocols for topical repellency (USDA 1977) and spatial repellency (attraction inhibition) in both competitive and noncompetitive bioassays (Gouck et al. 1967, Schreck et al. 1970, Kline et al. 2003). We chose the popular repellent deet to serve as the standard by which comparisons of repellency were made.

Materials and Methods

Chemicals. Chemical reagents are listed with the Chemical Abstracts number in brackets following the chemical name. Acetone [67-64-1] >99.5% A.C.S. reagent grade was purchased from Aldrich (Milwaukee, WI). L-(+)-Lactic acid [79-33-4] >99% was purchased from Fluka (Milwaukee, WI). A 2 μg/μl L-lactic acid stock solution was prepared in reagent grade methanol UltimAR [67-56-1] >99.9% (Mallinckrodt Chemical, Phillipsburg, NJ). Carbon dioxide [124-38-9] was delivered from a compressed gas cylinder (Airgas South Inc., Gainesville, FL). Deet [134-62-3] was obtained from our stock supply (Virginia Chemical Inc., Portsmith, VA) and prepared as a 25% (vol:vol) solution in ethanol [64-17-5] (190 proof, for Molecular Biology, Aldrich). Catnip oil (Canadian catnip) consisting of ≈80% nepetalactone plus nepetalactone isomers was purchased Essential Oil University (New Albany, IN).

Attraction and Attraction Inhibitor Bioassays. Tests were conducted in a triple cage, dual-port olfactometer (Posey et al. 1998). Each cage allows for a single experiment to be conducted. The mosquitoes either remain in the cage or fly upwind to be captured in one of the two ports, each containing either a treatment or control substance.

Air drawn from outside the laboratory was filtered, cooled or heated, and humidified or dehumidified as necessary by the air handling system to produce a constant air flow (28 ± 1 cm/s) maintained at 27 ± 1°C and 60 ± 2% RH through the selected test cage of the olfactometer. Approximately 75 nulliparous female 6- to 8-d old *Ae. aegypti* were selected for each test cage from a hand-draw box, and a specifically designed trap (Posey and Schreck 1981) was used to collect the mosquitoes and load them into each of the cages. Bioassays were conducted four times per day (0900, 1100, 1300, and 1500 hours, local time). Mosquitoes were loaded and allowed to acclimate in the olfactometer at least 45 min before each of the bioassay times. During this acclimation period, a low flow of air was passed through the ports into each of the olfactometer cages.

Treatments were randomized with respect to order, ports used, time of day, and cage within a complete block design. A total of six replicate tests were made for each treatment. A total of 11 treatments were used in the noncompetitive bioassays, and 12 treatment combinations (comparisons) were used in the competitive bioassays. The mosquitoes trapped in each of the ports, and those remaining in the cage were counted after each 3-min bioassay. Data were recorded as a percentage of the mosquitoes attracted to each port out of the total number of mosquitoes initially in the cage. Treatments consisted of 500 μl of catnip oil, 500 μl of deet, 5 ml/min carbon dioxide (Gillies 1980), the binary blend of 200 μg of L-lactic acid plus 500 μl of acetone (Bernier et al. 2003), and combinations of catnip oil or deet plus carbon dioxide, L-lactic acid and acetone, and odors from the arm of a human subject. The dosage of were selected to provide a dose of deet equivalent to 1 ml of a 50% deet product. The dosage of catnip oil was chosen to provide a sufficient dose of nepetalactone for an observed effect. As little as 50 μl of this substance produces inhibition (U.R.B., unpublished data). The binary blend composition and dosage was selected from previous experiments (Bernier et al. 2001, 2003). All chemical samples, except carbon dioxide, were dispensed onto a porous plastic block made of polyethylene and polypropylene (GenPore, Reading, PA) and manufactured for controlled release of 1-octen-3-ol in the field (Armatron International, Melrose, MA). Carbon dioxide was delivered from a cylinder, through a finely controllable metering valve (Nupro Co., Willoughby, OH) and measured on a calibrated flowmeter set to deliver 5 ml/min. In noncompetitive tests, the blank port contained a slow release dispenser, but no treatments. Both the blank port and treatment ports have an identical flow of conditioned air through them. Provided that there is no contamination, very few if any mosquitoes were trapped in this control port during the course of an experiment. Data presented in tables are untransformed means. Percentages were arcsine transformed before analysis.

Repellency Bioassays. Repellency, reported as minimum effective dosage (MED), was determined according to standard protocol (USDA 1977). The MED is the lowest dosage that resulted in three or fewer bites through a repellent-treated cloth, which is held above, but protected from contact with skin. Stock solutions of catnip oil and deet (50 mg each) were dissolved into 75 ml of ethanol in a 2-dram vial. Twofold serial dilutions of the stock solutions were made in ethanol to produce 10 treatment dosages that ranged from 1.0 to 0.001 mg/cm^2 when applied to muslin cloth. Cloth was treated by placing a rolled bandage (50 cm^2) into each vial to absorb the solution.

The cloth was stapled over a 4 by 9-cm opening cut into a file card (12.7 by 20.3 cm). The cloth was air-dried 15 min before conducting each test. The work reported here is an average of the MED for two volunteers. Each volunteer covered his or her arm with a nylon stocking to avoid contact between the skin and the treated cloth and wore a rubber glove to prevent mosquito bites on the hand.

A test consisted of a human inserting for 1 min the arm covered with treated cloth into a cage containing 200 female 7- to 16-d-old mosquitoes each of *Ae. aegypti*, *Anopheles albimanus* Weidemann, and *Anopheles quadrimaculatus* Say. If four bites were received by

Table 1. Noncompetitive olfactometer bioassays reported as percentage of attraction of female *Ae. aegypti* to single and combined treatments

Treatment	*n*	Mean ± SE
L-Lactic acid + acetone	6	48.0 ± 4.6a
L-Lactic acid + acetone + deet	6	36.5 ± 3.9ab
Left arm + catnip oil	6	36.0 ± 1.5ab
Left arm + deet	6	32.3 ± 4.4ab
Left arm	6	22.8 ± 4.3bc
CO_2 + deet	6	11.3 ± 2.9c
CO_2 + catnip oil	6	9.5 ± 1.4c
CO_2	6	9.0 ± 6.6c
L-Lactic acid + acetone + catnip oil	6	7.6 ± 3.1c
Deet	6	6.1 ± 1.5c
Catnip oil	6	6.1 ± 1.5c

Responses differed significantly with treatment (ANOVA; F = 17.18; df = 10, 55; $P < 0.0001$). Treatment means followed by the same letter are not significantly different using Tukey's standardized range test (P = 0.05). Each replicate consists of ≈75 female mosquitoes.

mosquitoes biting through the cloth to reach the arm, then the candidate repellent was considered to have failed at that dosage level. The repellent-treated cloth was evaluated at 15 min, removed, and stored in the laboratory under ambient conditions, and then affixed on the arm again at 24-h posttreatment and tested again. Written informed consent was obtained for all human subjects used in this study in accordance with protocol #460-2002, as approved by the University of Florida, Health Sciences Center, Institutional Review Board for Human Subjects.

Data Analysis. Treatment means in noncompetitive olfactometer assays were analyzed by analysis of variance (ANOVA) followed by Tukey's standardized range tests for separation of means ($P < 0.05$) (SAS Institute 1999). Means from competitive olfactometer bioassays were analyzed using paired t-tests ($P < 0.05$). The repellency MEDs are reported as simple means of the MEDs observed by each volunteer.

Results and Discussion

Noncompetitive Olfactometer Bioassays. In noncompetitive tests (Table 1), the binary blend of L-lactic acid and acetone was the most attractive treatment; however, the addition of deet only slightly (25%) reduced the mean attraction level, and this reduction was not statistically significant ($P > 0.05$). Although it is possible that deet inhibited the effect of lactic acid as reported by Dogan et al. (1999), because this is a binary blend the high level of acetone may offset the reduction in attraction that would otherwise be expected with inhibition of the lactic acid receptor. In contrast to the effect of deet, catnip oil was a highly effective inhibitor when combined with the blend, as evidenced by the 80% reduction in attraction of the level observed from the blend without catnip oil.

The attraction to human odors increased when combined with either of the test repellents; however, addition of catnip oil or deet failed to increase the mean response significantly ($P < 0.05$). Although the increased attraction response to human odors in combination with deet and catnip oil was unexpected, the human volunteer in this study has been shown to exhibit the lowest overall attraction to *Ae. aegypti* of any volunteers used in previous experiments (Bernier et al. 2001; U.R.B., unpublished data). We hypothesize that this may have resulted in the increased attraction response when combined with the inhibitor and repellent and a follow-up study to test this is planned. As was the case with the chemical blend, the deet inhi-

Table 2. Comparison of chemical attractants in competition with the identical composition of attractants plus catnip oil in olfactometer bioassays

Treatment	Alone Mean ± SE (%)	+ Catnip oil Mean ± SE (%)	t^a	$P > t$
Acetone	45.3 ± 4.9	4.2 ± 1.1	7.76	<0.0001
CO_2	28.8 ± 7.0	10.1 ± 1.6	2.62	0.01
L-Lactic acid + acetone	41.4 ± 5.4	4.3 ± 0.7	6.68	<0.0001
Human arm (left vs. right)	47.5 ± 3.1	13.0 ± 0.7[b]	10.16	<0.0001

[a] Means were tested using paired t-tests ($P < 0.05$). Means represent six replicates each consisting of ≈75 female mosquitoes.

[b] Catnip oil was applied to the left arm, and ethanol was applied to the right arm.

Table 3. Comparison of chemical and human odor attractants plus catnip oil in competition in olfactometer bioassays against catnip oil alone

Treatment	Mean ± SE (%)	t	P
Human arm (left) + catnip oil	39.9 ± 5.0	7.36	<0.0001
Catnip oil	0.5 ± 0.3		
CO_2 + catnip oil	13.2 ± 2.4	1.24	0.120
Catnip oil	9.3 ± 2.0		
L-Lactic acid + acetone + catnip oil	13.7 ± 3.6	1.37	0.100
Catnip oil	7.8 ± 2.3		

Means were tested using paired t-tests ($P < 0.05$). Means represent six replicates each consisting of ≈75 female mosquitoes.

Table 4. Comparison of catnip oil to deet where both are used as inhibitors and tested alone or coupled with various chemical attractants in olfactometer bioassays

Treatment	+ Catnip oil Mean ± SE (%)	+ Deet Mean ± SE (%)	t	P
None additional	7.9 ± 1.8	13.8 ± 1.5	2.49	0.01
CO_2	9.9 ± 2.3	30.3 ± 7.3	2.61	0.01
L-Lactic acid + acetone	6.7 ± 1.4	21.3 ± 4.5	3.12	0.005
Human arm (left vs. right)[a]	15.6 ± 2.4	35.6 ± 4.6	3.78	0.002
Human arm (right vs. left)[b]	16.9 ± 2.9	36.2 ± 3.5	4.02	<0.0001

Means were tested using paired t-tests ($P < 0.05$). Means represent six replicates each consisting of ≈75 female mosquitoes.

[a] Odors from the left arm of the human volunteer are paired with catnip oil and compared with odors from the right arm with deet.

[b] Odors from the right arm of the volunteer are paired with catnip oil and compared with odors from the left arm with deet.

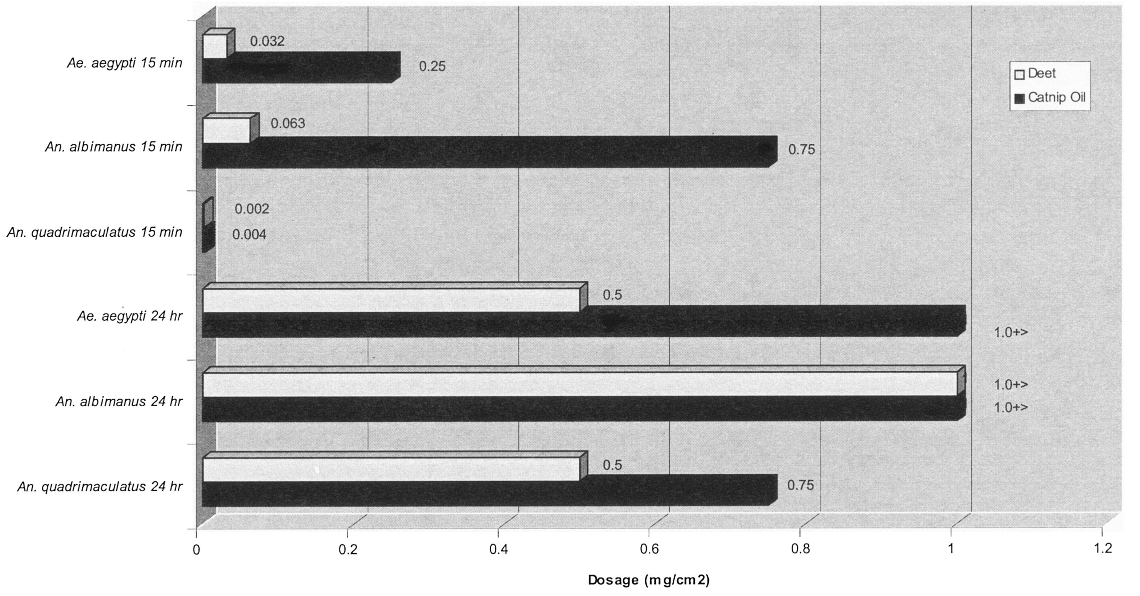

Fig. 1. Mean MED at 15 min and 24 h posttreatment application on 5 by 10-cm muslin cloth patches. Data represented as $\geq$1.0 mg/cm^2 indicate it would take a higher dose to be effective and prevent mosquito bites than the highest dose tested (1.0 mg/cm^2).

bition of the lactic acid receptor and other attractant receptors may not be expressed on a behavioral level because other cues may still result in attraction. No significant differences existed in the mean percentages of mosquitoes attracted to carbon dioxide alone, deet alone, catnip oil alone, carbon dioxide combined with deet, and carbon dioxide combined with catnip oil. Deet and catnip oil both were weak attractants; however, it was expected based on previous research (Mehr et al. 1990, Dogan et al. 1999) that deet would show some attraction at low doses and in the absence of other chemical stimuli.

Interpretation of results from noncompetitive bioassays may be problematic because in the absence of a competitive blend of odorants, mosquitoes may respond abnormally, i.e., when presented with only one choice, a larger proportion of the test population may respond to a blend of odorants than when the choice involves two different treatments. The presentation of a single stimulus, although designed to pinpoint the behavioral effect by minimizing the variables such as odor stimuli, may elicit unnatural behavior in the mosquitoes because mosquitoes are capable of discerning complex odor profiles in the wild and orient toward a preferred host. Additionally, the introduction of chemical attractants at much higher release rates can result in a greater efficiency of collection of mosquitoes, even though these attractants may not be as attractive when tested against human odors (Bernier et al. 2001).

Competitive Olfactometer Bioassays. In the wild, mosquitoes are capable of discerning host odors in competition with other odors found in the environment. Thus, a situation whereby mosquitoes can select between odor sources may more accurately reflect the process of attraction and or inhibition that occurs under natural conditions. The primary concern with conducting competitive bioassays involving inhibitors in this type of olfactometer is that the effect of an inhibitor in one port may influence all of the mosquitoes in the cage and affect the results, or catch, in the second port (Dogan and Rossignol 1999). An observed reduction in total catch in both ports is an indication of the masking capability of the inhibitor and was observed and described previously (Kline et al. 2003).

Bioassay results for attractants with and without catnip oil are shown in Table 2. In all cases, the presence of catnip oil decreased attraction to the port containing attractants plus this oil. The differential distribution of mosquitoes between ports was larger for chemical attractants, such as acetone and the blend of lactic acid and acetone, in comparison with human odor and for carbon dioxide. These results are expected because human odors in competitive tests (Table 2) are generally more attractive to mosquitoes than are synthetic chemicals. Therefore, human odors are more difficult to mask than synthetic chemicals. CO_2 is a weaker attractant than human odors, and in the absence of a synergist, there would be a smaller difference in catches between two ports with a weak attractant. In this olfactometer, CO_2 does not attract high proportions of test mosquitoes unless there is contamination of the ports with human odors (Bernier et al. 2003).

Comparisons of catnip oil combined with attractants against catnip oil alone are shown (Table 3). Even when catnip oil is combined with human odors, the catch in the port with these human odors is $\approx$2 orders of magnitude greater than catnip oil alone. Unlike the comparison of human odors plus catnip oil against human odors (Table 2), the comparison of odors plus catnip oil against catnip oil, makes a comparison to catnip oil, a much weaker attractant. Therefore, the mosquitoes overwhelmingly chose the port with odors present.

Neither carbon dioxide nor the binary blend of lactic acid and acetone showed a distribution so heavily favored toward the attractants. The most likely reason is that these chemicals are less attractive to mosquitoes than are human odors. It also should be noted that mosquitoes in the cage were exposed to twice the dosage level of this inhibitor, because catnip oil is added to both ports.

Direct comparison of the attraction of catnip oil in competition against deet shows that deet is more attractive (Table 4). These findings support previous observations (Peterson 2001) that mosquitoes prefer a deet-coated surface over a nepetalactone-coated surface. Both carbon dioxide and the binary blend of lactic acid and acetone are much less preferred when combined with catnip oil than when combined with deet. The preference for human odors was $\approx$2:1 in favor of the odors combined with deet over odors combined with catnip oil. We chose to compare odors from a set of repetitions by using the left arm against right arm with an inhibitor on each side to a set of repetitions with the inhibitors reversed to examine for an effect due to left or right-handedness of the volunteer. Notably similar results were obtained when the inhibitors were reversed in proximity to the left and right arm (Table 4). Similar responses were reported previously (Kline et al. 2003) when an identical attractant blend was placed in each port and tested in this olfactometer.

Repellent Activity Screening Trials. Two volunteers screened catnip oil and deet by using a standard protocol for screening repellents (USDA 1977). The average MED values at 15 min and 24 h posttreatment, against three species of mosquitoes, are found in Fig. 1. Against *Ae. aegypti,* deet was the more effective repellent at the 15-min interval, needing a factor of 8 lower dosage to repel this species. The MED for the 24-h test indicated that deet was effective at 0.5 mg/cm^2, whereas catnip oil required an application dosage of >1.0 mg/cm^2. At the 15-min posttreatment mark, catnip oil required a much higher dosage (0.75 mg/cm^2) for effective protection against *An. albimanus,* whereas deet only required 0.063 mg/cm^2 to remain effective. Both substances failed at the 1.0 mg/cm^2 dosage level at the 24-h mark against this species of anophelines. Both candidate repellents were most effective against *An. quadrimaculatus.* For this species, a very low dose of deet (0.002 mg/cm^2) and catnip oil (0.004 mg/cm^2) was effective at 15 min, and 0.5 mg/cm^2 deet and 0.75 mg/cm^2 catnip oil were required at 24-h post treatment.

We conclude that deet and catnip oil are weak attractants, in the absence of other odors, when exposed to female *Ae. aegypti* mosquitoes. Catnip oil was more effective in attraction inhibition or as a spatial repellent than deet with respect to masking chemical attractant and human odors from *Ae. aegypti* mosquitoes. Deet was the more effective topical repellent than catnip oil by using a treated cloth patch in repellent screens against *Ae. aegypti, An. albimanus,* and *An. quadrimaculatus* species of mosquitoes. It should be noted, however, that catnip oil did exhibit properties of topical repellency, and this oil and its components, particularly nepetalactone isomers, merit further examination both as spatial and as topical repellents for mosquitoes.

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